

NOTES ON THE NATURAL HISTORY OF  
*MORPHO GRANADENSIS POLYBAPTUS* BUTLER  
(LEPIDOPTERA: NYMPHALIDAE: MORPHINAE),  
AND ITS RELATION TO THAT OF  
*MORPHO PELEIDES LIMPIDA* BUTLER

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*Abstract.*—Various aspects of the natural history of the Neotropical butterfly *Morpho granadensis polybaptus* Butler (Lepidoptera: Nymphalidae: Morphinae) in a zone of geographical overlap with *M. peleides limpida* Butler in Costa Rica are reported for the first time. The work reported is part of a long-range study on the comparative natural history of Central American *Morpho*, represented in Costa Rica by at least five valid species. Of particular interest is the comparison of *M. granadensis* with *M. peleides* since both species are closely related forms in the South American *achilles* "superspecies" complex. *Morpho granadensis* is exceedingly rare in museum collections and the type specimen is from Costa Rica. The species is narrowly restricted in Costa Rica to a band of tropical rain forest within about 100 to 600 meters elevation along the Caribbean watershed of the Cordillera Central and adjacent highlands. The early stages are strikingly similar to those of *M. peleides*, including various aspects of caterpillar behavior. Oviposition is single. Although the caterpillars are legume-feeders, either the scope of food plant suitability is narrower or different between this species and *M. peleides*, since the former cannot survive on at least one common food plant (*Mucuna urens*) of the latter. *Morpho peleides* has a much wider geographical range than *M. granadensis*, and probably utilizes a greater range of food plants. The species is also sympatric with *M. amathonte* Deyrolle; baiting studies indicate that *M. granadensis* is about half as abundant as the other two species. A model for further comparative study of the two species is presented.

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Introduction

Some of the seminal papers on the life cycles and natural history of various species of *Morpho* butterflies (Lepidoptera: Nymphalidae: Morphinae) in Central America have appeared recently on the pages of this journal (e.g., Young 1972a; Young and Muysshondt 1972a) and elsewhere (Young 1971a, b, 1972b, 1973, 1974, 1975a, b, 1978b, 1979, 1980a; Young and Muysshondt 1972b, 1973; Young and Thomason 1974). As part of a long-range goal of studying the biology of all Central American species of this widespread

Neotropical genus, field studies were conducted on *Morpho granadensis polybaptus* Butler in northeastern Costa Rica, in a region where this species and another one of the *achilles* "superspecies," *Morpho peleides limpida* Butler, are sympatric. Of particular interest is the study of *M. granadensis polybaptus* in Costa Rica, the site of the type specimen for this species (Seitz 1924). This paper reports the first description of the early stages and larval food plant association for this species, and compares these attributes and others with previously reported data on *M. peleides* from Costa Rica (Young and Muyschondt 1973; Young 1972a, b, 1978b; and other papers). Because adults of both species are very similar (Fig. 1), and one species (*peleides*) is far more abundant than the other in zones of geographical overlap, studies on the comparative natural history of these forms is of particular interest, in the context of recent discussions of ecological mechanisms of environmental exploitation among closely related sympatric species (e.g., see MacArthur 1972).

The major findings of this paper are the following: (1) the early stages of *M. granadensis* are strikingly similar morphologically and behaviorally to those of *M. peleides*, (2) one larval food plant of *M. granadensis*, the woody vine *Machaerium seemannii* (Leguminosae) is also one of several leguminous larval food plants of *M. peleides* in this region (Young and Muyschondt 1973) but caterpillars of *M. granadensis* die in early instars when reared on several of these other plant species, suggesting a narrower range of food plants in *M. granadensis*, (3) the egg-to-adult developmental times are very similar in both species, (4) overall average egg production is probably much lower in *M. granadensis* as captive females are less prone to oviposit and lay fewer eggs when they do, and (5) *M. granadensis* has a relatively restricted distribution within a narrow band of Caribbean watershed tropical rain forest within about 100 to 600 meters elevation, while *M. peleides* is far more catholic in its distribution throughout the whole country. Furthermore, *M. granadensis*, although very similar in habitat association and natural history to *M. peleides*, is probably not as abundant locally as the latter. Along with *M. amathonte* Deyrolle, both species readily come to bait (rotten bananas) although sex ratios are invariably skewed towards males (see also Young 1974, 1975a; Young and Thomason 1974; Young 1972a). Based on this study and several previous ones (as cited above), a general model for ecological segregation in zones of sympatry among the five species of *Morpho* in Costa Rica is presented as a testable set of hypotheses for further study.

### Methods

*Morpho granadensis* was studied at "Finca La Tigra," a locality within the premontane tropical wet forest zone of northeastern Costa Rica, and



Fig. 1. Dorsal and ventral aspects of *Morpho peleides limpida* (left column) and *M. granadensis polybaptus* from northeastern Costa Rica. Specimens part of reared and wild-caught series in the collections of the Milwaukee Public Museum.

about 10 km east of La Virgen (10°23'N, 84°07'W; about 220 m elev.), Heredia Province. This locality is about 15 km west of the site where I originally found *M. granadensis* (Young 1972a), the first known collection of this species since its original discovery in Costa Rica in 1904 (specimen in the Allyn Museum, a male, collected by A. Hall, at "Castillo"). This original locality is probably Castilla (10°43'N, 85°25'W). Through baiting (with rotten bananas) within the mixed primary-secondary tropical rain forest at La Tigra (Fig. 2), it was possible to obtain a new series of specimens and mated females. Collecting of new material was kept to an absolute minimum. Periodically between 1977 and 1981, I baited *M. granadensis*, along with *M. peleides* and *M. amathonte* within an approximately 2,000 square-meter plot of forest, placing three piles of rotting bananas at scat-





Fig. 2. View through the light-gap associated with the plot of mixed primary and secondary premontane tropical rain forest at "Finca La Tigra" in northeastern Costa Rica where *Morpho* butterflies were baited with rotten bananas over several years. Adults of at least three species (see text) occur in this habitat. It borders on a cacao plantation created largely by "tunnelling" of advanced secondary forest to allow room for cacao trees.

tered places along two different foot paths within this area. Baits were always placed at the same places as I was interested in estimating the relative abundance of the three species in various months at this somewhat seasonal (although very irregular) locality (Fig. 3). The baiting also provided fecundated females from which to obtain fertile ova for rearing studies. I did not attempt to make a thorough study of abundance and temporal distribution on a daily basis (e.g., Young 1972a), but rather only collected or observed butterflies at baits whenever possible.

I used the bagging method described earlier (Young 1978b; Young and Muyschondt 1973) to rear caterpillars. Generally I obtained fertile ova by confining a freshly-caught female in a large clear plastic bag containing fresh cuttings of various suspected leguminous food plants (candidates taken from the list generated in Young and Muyschondt 1973 for *M. peleides*) and keeping each bag tightly closed. In this manner butterflies were kept for one to three weeks, during which each was fed daily outside the bag with rotten bananas. The cuttings were replaced as needed, fresh ones sprayed with water, and eggs removed at regular intervals. With *Morpho*, this technique is very successful. I deliberately tested samples of first instar larvae within



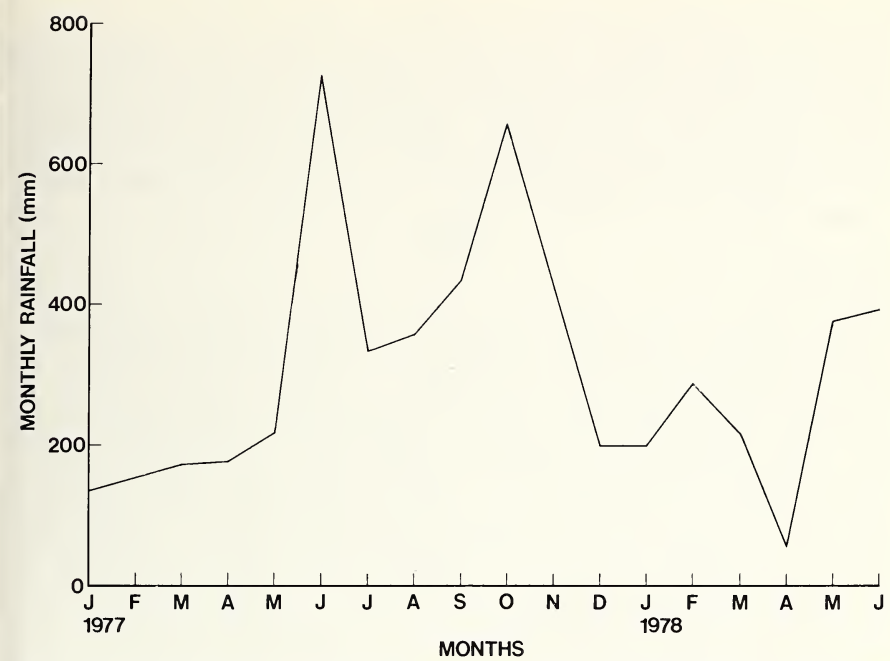


Fig. 3. A typical pattern of rainfall during which some of the studies were made at Finca La Tigra. Note the general depression of rain during January, February and March, and a second, less lengthy dip in April. This pattern is fairly typical over a run of several successive years.

each batch of eggs obtained in this manner on different suspected larval food plants, with an emphasis on comparing larval performance (survival, growth rates) on two major food plants of *M. peleides*, *Mucuna urens* and *Machaerium seemannii*, both stout woody legume vines associated with forest-edge and secondary habitats (see Young and Muyshondt 1973) in Costa Rica. I also obtained a third-instar larva of *M. granadensis* (determined to be this species from rearing to adult stage) from Philip J. DeVries, who found it on a small "trailside" seedling of *M. seemannii* at "Carillo" (San Jose Province, 600 m elev.). This discovery by Mr. DeVries constituted the only wild record of the species on a particular food plant, as all of my information on life cycle was generated by the rearing of larvae from ova obtained from captive females. Whenever possible, I reared *M. peleides* simultaneously with *M. granadensis*, and using the same food plant material. Because both species are closely related in the *achilles* Linnaeus "superspecies" complex of South America (see Young 1974), I suspected overlap in larval food plants when these rearing tests were initiated.

Additional material was reared independently by Philip J. DeVries, using

eggs or larvae collected either at Carillo or "Finca La Selva," the site of my original field study on the adults of this species and others (Young 1972a). In addition to the three species mentioned thus far, two others, *M. theseus* Deyr. and *M. cypris* Westw., are also found at the La Tigra locality. The locality has been the site for studies on the natural history of other forest-associated day-flying Rhopalocera (e.g., Young 1977, 1978a, 1980b).

## Results

### Distribution

Based upon my own observations in Costa Rica (1968–81) and those of Philip J. DeVries (several pers. comms.), *M. granadensis* is probably distributed within a relatively narrow band of tropical rain forest along the Caribbean watershed of the Cordillera Central, between 100 and 600 meters above sea level. Because specimens of this form are exceedingly rare in museum collections throughout the world, there are few data available on distribution. In Costa Rica, the species is associated with the "Carrillo belt" (see DeVries 1980), extending to the north slopes of the Poas volcano and south to the Reventazon River Valley. Populations probably follow the series of ridges along this imaginary transect. It is probably not found in the lowland coastal areas of the Caribbean watershed and it is absent from the Pacific side of the country, even where tropical rain forest is well developed (e.g., Corcovado National Park on the Osa Peninsula). In contrast, *M. peleides* is widely distributed in several major climatic zones of Costa Rica (Young and Muyschondt 1973; Young and Thomason 1974) and it is one of the most widely distributed species throughout much of Central America, not to mention the broad distribution of related forms in South America (Seitz 1924). Unlike *M. granadensis*, specimens of *M. peleides* from specific localities exhibit considerable marked variation in the markings on the undersides of the wings (A. M. Young pers. obs.). Such variation is often associated with a single batch of eggs (pers. data). The extreme variation in wing markings and coloration in this species has been emphasized (Seitz 1924) and it exists both within and between populations. *Morpho granadensis* has a much more restricted geographical distribution in southern Central America and northern South America (Seitz 1924) and specimens generally lack, in my experience, the marked phenotypic variation so prevalent in *M. peleides*. Further field study in Central America should focus upon the determination of distribution boundaries of *M. granadensis*, suspected to include Nicaragua and Panama (Seitz 1924). The several specimens I have reared over the past four years match very well the two male specimens in the Allyn Museum collection (the forementioned specimen from A. Hall and that of W. J. Kaye, collected at "Pejeballe" in 1926).

## Early Stages

The early stages are very similar to those of *M. peleides* (see Young and Muysshondt 1973). Detailed taxonomic separation and a key to early stages in these species and other is awaiting completion of life cycle studies of all Central American species. A good series of eggs and caterpillars for *M. granadensis* and *M. peleides* is available with the author. Some general features are described here. The egg is green and within two days after being deposited, develops a lateral reddish-brown band (Fig. 4). Unlike that of *M. peleides*, this band is distinctly broken into small dots (Fig. 4). But at Corcovado National Park in southwestern Costa Rica, the egg band of *M. peleides* is also broken (P. J. DeVries pers. comm.). Egg hatches in 16 days and first instar is yellow and red (Fig. 4). The second instar (Fig. 4) is similarly patterned but with a marked change in the distribution, coloration, and sizes of setae. For example, distinct rows of long white setae appear at the posterior margins of the second and third thoracic segments (Fig. 4). Setae generally black and evenly distributed on most body segments in the first instar. The second instar develops a set of dorso-lateral groupings of long, filamentous red and white setae on the posterior five abdominal segments, and all body segments have long, whitish lateral setae as well (Fig. 4).

The first instar head capsule of *M. granadensis* possesses a greater number of setae than does that of *M. peleides* (Fig. 5). The medial edge of the mandible in *M. granadensis* (first instars) possesses relatively short protuberances compared to that of *M. peleides* (Fig. 5). The cuticle over most of the head capsule in *M. granadensis*, and exemplified by the area just above the ocelli region, is finely studded with many small protuberances while that of *M. peleides* is relatively smooth (Fig. 6). These micromorphological distinctions in the head capsule appear to be very consistent in separating the first instar caterpillars of these two species.

The third instar is very similar to the second instar, but with further shortening of head capsule setae in the former (Fig. 7). Early instars generally rest on leaves of *Machaerium seemanii* when not feeding (Fig. 7). As in *M. peleides* (Young and Muysshondt 1973), there is a major change in the coloration of the caterpillar in the fourth instar (Fig. 7). The caterpillar becomes shaded in rich hues of brown, pink, and white. There is further reduction and coalescence of setae into sets of distinct tufts (Fig. 7) and the caterpillar generally rests on woody stems of *M. seemanii* when not feeding. The fifth instar is similar to the fourth, but with colors becoming more bland and setae reduced in size. Prior to developing into a highly mobile green prepupa of contracted size, the caterpillar attains a length of about 100 mm and maximal width (laterally) of about 20 mm. The caterpillar stage, as measured on a total of 16 individuals reared, lasts 89–96 days. These estimates may



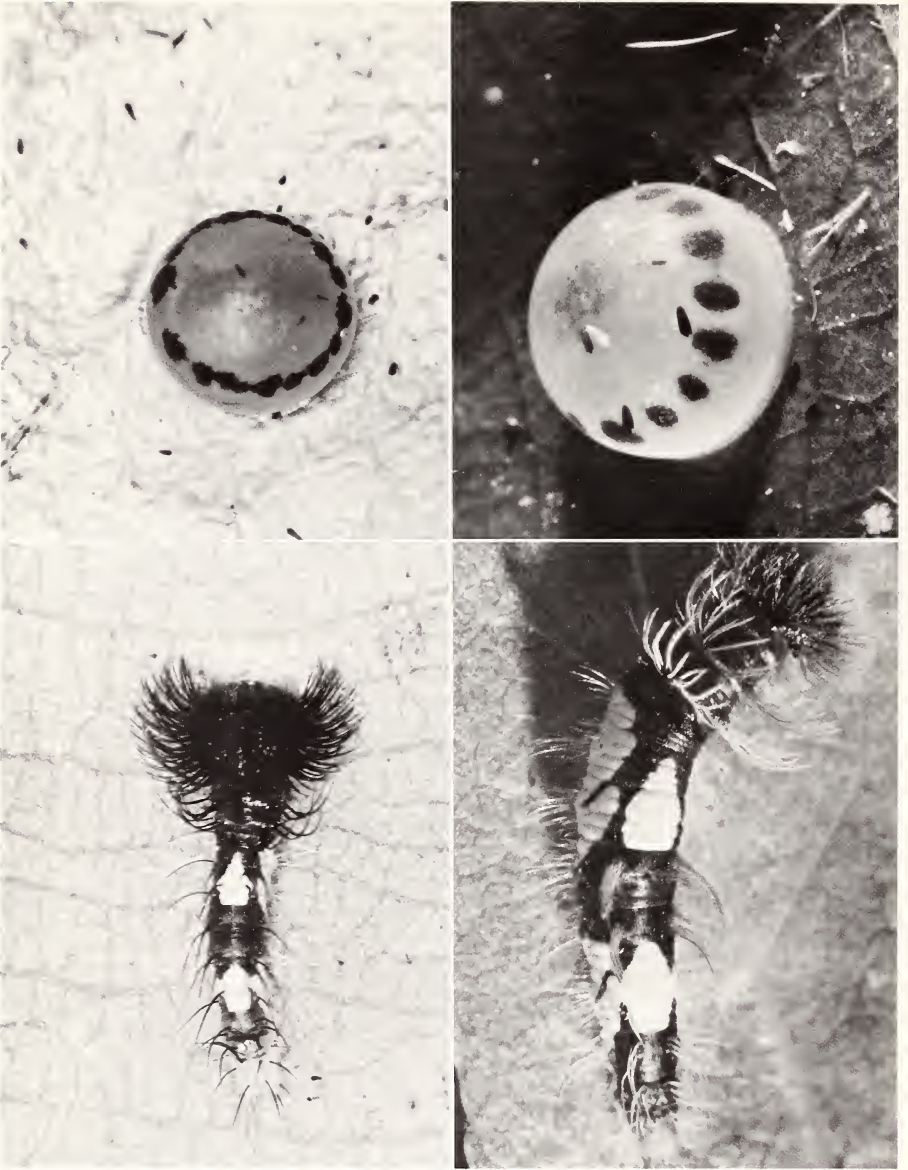


Fig. 4. Early stages of *Morpho granadensis*. Top: egg; note broken "ring" of brownish pigmentation of the hemispherical green egg (about 1.8 mm dia.). Bottom, left to right: first and second instar caterpillars respectively.

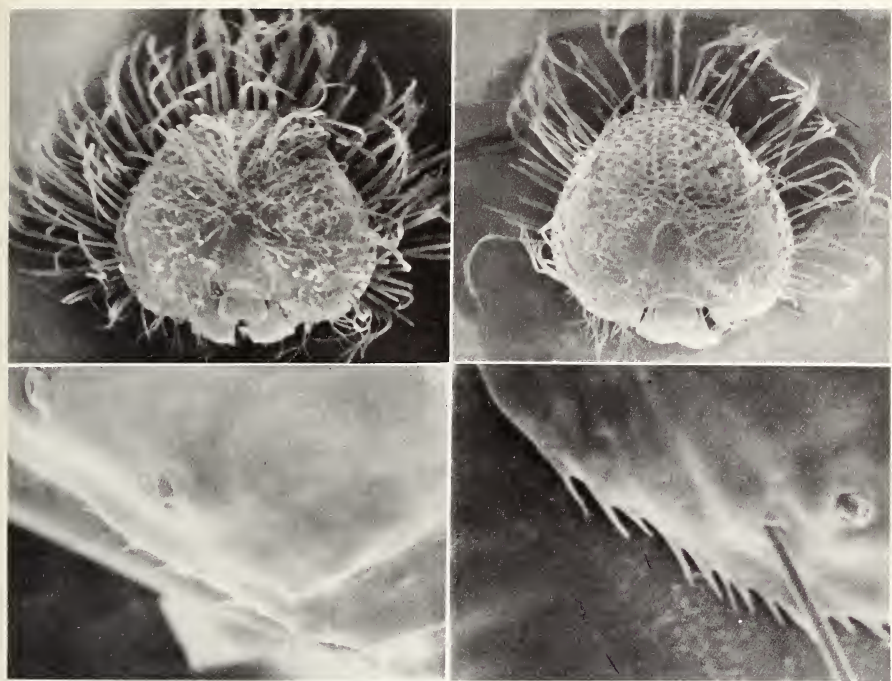


Fig. 5. Some micromorphological differences between the first instar caterpillars of *M. granadensis* and *M. peleides*. Left column: head capsule (SEM, 20× mag.) and right mandible (1,000× mag.) for *M. granadensis*. Right column, same structures and magnifications, but for *M. peleides*. Preparations and SEM work by R. Wolff.

have relatively little biological significance since caterpillars were often transported around considerably while being reared, and therefore subject to different environmental conditions.

The pupa (Fig. 7) is uniformly green with a pinkish-brown cremaster. It is 34–38 mm long and with a maximal dorso-ventral width of 15.5 mm and lateral width of 16.5 mm. Three prominent spiracles adjacent to the wing pads are white, while others are much smaller and pinkish. The marked protuberances of the head region are deep brown or black. The pupa stage lasts about 24 days. Eclosion is extremely rapid, with the wings fully expanded within one hour. Newly eclosed males less than two days old exude a rich fragrance similar to that of rancid margarine.

Behavior

Oviposition-proneness in *Morpho* refers to the readiness of captive fecundated females to deposit eggs on larval food plant cuttings. Females of

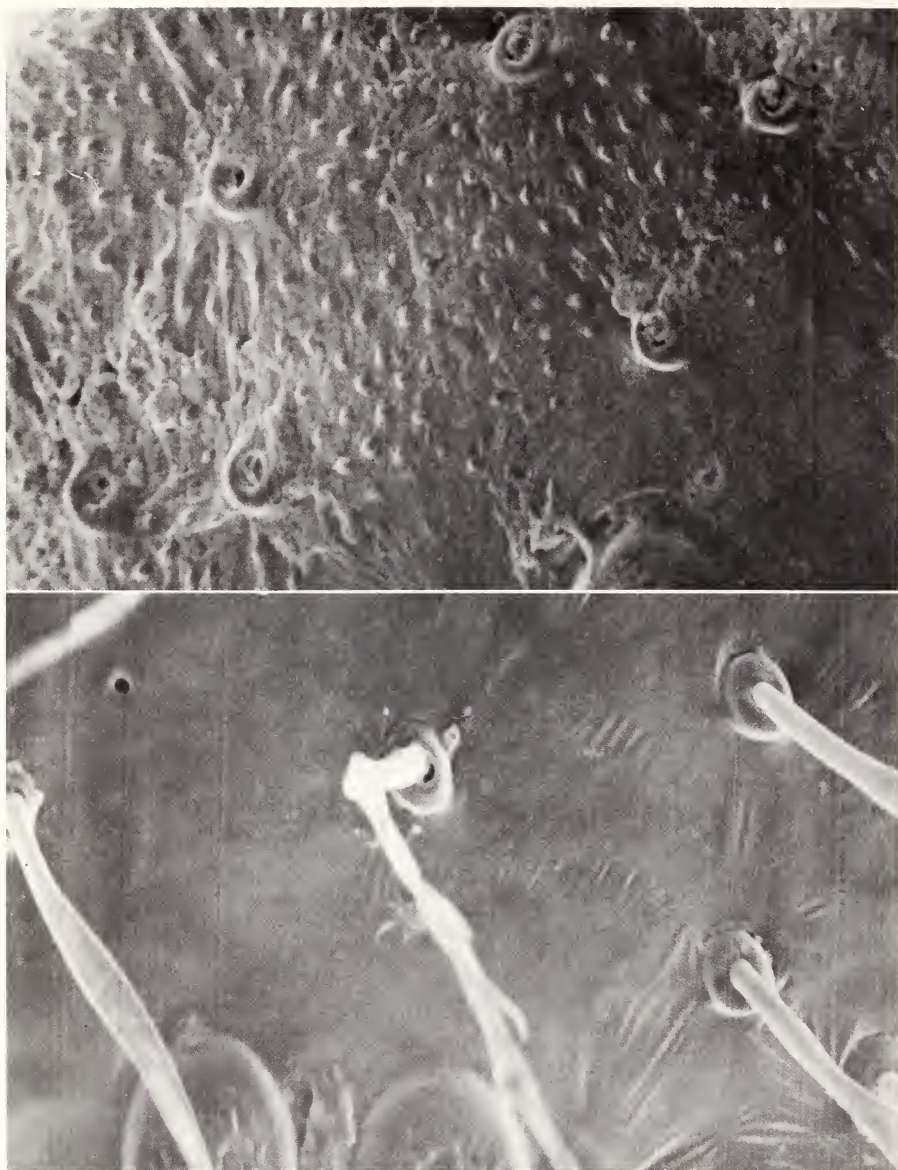


Fig. 6. Sculpturing of the cuticle of the head capsules of first instar caterpillars of *M. granadensis* (top) and *M. peleides* (below) for medial-lateral sections above region of ocelli (500 $\times$  mag., with SEM). Preparations and SEM work by R. Wolff.





Fig. 7. Early stages of *Morpho granadensis*. Top, left and right: third-instar caterpillars resting on leaves of a larval food plant, *Machaerium seemannii* (Leguminosae). Note leaf damage from feeding in the photograph to the right. Bottom: fourth instar caterpillar (left) and pupa (right).

*M. granadensis* generally require two to four days before egg-laying is initiated under these conditions, while the response is generally less than two days in *M. peleides*. Successful mating cannot be achieved by confining a virgin female with an active male in a clear plastic bag. In one such test, the two butterflies were kept active for about two weeks without copulation taking place. The female was clearly a virgin given the large amounts of body fluids exuded in the first few days of confinement, indicating a very recent eclosion. Given tests with both *M. granadensis* and *M. peleides*, it is likely that mating takes place very soon after eclosion in the wild. In captivity, eggs are placed singly on the food plant, and it is known that oviposition is single in the wild in *M. peleides* (Young and Muyschondt 1973). I suspect single oviposition in *M. granadensis* in the wild.

Adults of both species regularly show up at fruit baits (see below) and can sometimes be distinguished by the amount of blue reflectance and size of the wings. At a closer distance, the distinctive coloration of the ocellus markings on the ventral sides of both sets of wings between the two species is very evident (see also Fig. 1). In *M. granadensis*, both the circulus and ocellata associated with each of the three eyespot markings on each forewing, and the set of four such markings on each hindwing are colored in vivid reddish-orange. In *M. peleides*, these areas are yellowish. In *M. granadensis*, the circulus is a very thin reddish-pink or slightly lavender line, while in *M. peleides* it is light blue. In *M. granadensis* the center spot of each eyespot marking is bluish while it is white in *M. peleides*. The number of eyespot markings on the forewings of individual specimens of *M. peleides* is often very variable while seldom so in *M. granadensis*. Relative to *M. peleides*, the dorsal marginal black border of both sets of wings is thinner in *M. granadensis*. Good descriptions of wing coloration for both species is given in Seitz (1924). The above comments are made more in the context of providing a key to an immediate identification of species in the wild. A detailed study of the evolutionary relationship between these two species must understandably await for a detailed study of the genus as a whole, including the examination of early stages and biogeographical patterns.

In laboratory culture, caterpillars of *M. granadensis* exhibit the same "dawn-dusk" feeding rhythm as do the caterpillars of *M. peleides* (see Young 1972b), with the dusk peak being greater than the dawn peak. Presumably similar behavior exists in the wild.

### Food Plant Preference

When offered various leguminous food plants, known to be acceptable to the caterpillars of *M. peleides* from sympatric Costa Rican populations, the first instar caterpillars of *M. granadensis* exhibit distinctive patterns of response. For example, of a total of 32 first instars offered fresh leaves of *Mucuna urens*, a very common food plant of *M. peleides* (Young and Muyschondt 1973),

shondt 1973), all died within five days, and following the actual ingestion of tissues along leaf edges. Similar results were obtained in tests of 17 first instars with the leaves of *Erythrina* sp. From studies of *M. peleides* (e.g., Young 1978b; Young and Muyschondt 1973) it is known that even first instars preferentially eat the tissues from older leaves of *M. urens* and other legumes, and *M. granadensis* in the present tests were offered both young and old leaves. Although *M. peleides* can be successfully reared to adulthood on the leaves of peanut, *Arachis hypogea* (Young 1974), results are more mixed with *M. granadensis*: in a total of 15 first instars tested, 10 died in that instar, two more survived to the next instar, and the others perished in the third instar (within two days following the molt). At the same time, all but two of an initial group of 12 *M. peleides* were reared to adulthood on the same peanut plants. Although these samples are exceedingly small, they do provide some tentative evidence of a differential response between these two species to legumes. The inference is that *M. granadensis* does not share all of its food plants with the closely related *M. peleides*. A total of 10 caterpillars of *M. granadensis* have been reared successfully on one common food plant of *M. peleides*, *Machaerium seemannii*. Furthermore, one partially-grown caterpillar was discovered feeding on this plant in the wild (Carillo, San Jose Prov., Costa Rica) by Philip J. DeVries, thus confirming this woody legume vine as a food plant of *M. granadensis* in Costa Rica. This species has also been reared at Finca La Selva by P. J. DeVries. Both butterflies share the habit of placing eggs on seedlings of *M. seemannii* (see also Young 1972a; Young and Muyschondt 1973) since the one caterpillar found in the wild was on a small seedling.

### Species abundances

The irregular program of baiting *Morpho* in the same tract of tropical rain forest over several years suggests that *M. granadensis* is less abundant than two other sympatric species, *M. peleides* and *M. amathonte* (Table 1). While samples are small and widely scattered over time, they do reflect the low density property of adult populations of these butterflies, as noted for *M. peleides* in tropical rain forest elsewhere in Costa Rica (Young 1973). In tropical wet regions populations of these butterflies tend to be of low adult densities, except when restricted to a small habitat (e.g., Young and Thomason 1974). The patterns of sex ratio observed in the present study (Table 1) are fairly typical for baited *Morpho*, in which males far outnumber females, regardless of the species (see also Young 1972a, 1973; Young and Thomason 1974). All three species were found to be active at various times of the year, including the drier months of February and March (Table 1 and Fig. 3). As noted in the footnotes to Table 1, there is considerable variation in the production of eggs by individual captive females of *M. granadensis*, although again samples are very small. Although hourly samples are not available, there is clearly considerable feeding at



baits during the afternoon hours (Table 1). Based upon a very limited mark-recapture study, there is some evidence that the same individual butterflies may appear at a bait on successive days. For example, the male *M. granadensis* sighted on 20 February 1980 was captured, marked (with a fast-drying white enamel paint—see Young and Thomason 1974 for details of this technique), and released immediately. This male was subsequently resighted at the three baits on 21 and 22 February. Similarly, two males of *M. peleides* marked and released on 22 February 1980 were resighted at the baits, and one of these was seen feeding the following day at noon (Table 1).

### Discussion

Because both *M. granadensis* and *M. peleides* are both members of the *achilles* "superspecies" complex (Young 1974), it is not unexpected that their early stages would be of similar appearance and behavior as reported in this present study. Yet consistent morphological differences, including larval characters, adult wing color patterns, and genitalia structure (Young unpubl. data), indicate the forms to be two valid species. Both undoubtedly represent the geographical extension of the *achilles* complex into Central America, although one, *M. granadensis* is far more restricted in this ecological range extension than the other. Elsewhere (Young and Muyschondt 1973), it is argued that *M. peleides* represents the form most successful in the colonization of secondary habitats in both the non-seasonal and seasonal tropical forest zones of Central America and Mexico. *Morpho granadensis*, in contrast, is a restricted tropical rain forest form associated with intermediate elevations along the Caribbean drainage of southern Central America, and the northern part of South America.

The topic of this paper is not to make an attempt to reconstruct what might have been the ecology of a progenitor form to both species, and the selection pressures leading to divergence. Rather, we are at the descriptive stage of trying to gather basic natural history data that provide some clues to present-day patterns of differentiation between the two species in a region of sympatry and ecological overlap. What is of interest in this context is the considerable overlap in the flying seasons of both species, their co-occurrence at baits in tropical rain forest, and a preference for the same habitat. Yet *M. peleides* is a far more widely distributed species than *M. granadensis*, suggesting indirectly that the two forms are not in direct competition for resources. Rather, I tentatively conclude that the ecological requirements of *M. granadensis*, particularly as related to the exploitation of larval food plants, represents a subset of those required by *M. peleides*. The data and other reports (Young and Muyschondt 1973; Young and Thomason 1974) suggest that *M. peleides* has a higher reproductive capacity (defined here

Table 1. Comparative abundance of three species of *Morpho* butterflies at baits of rotting bananas in an approximately 2,000 m<sup>2</sup> block of tropical rain forest in northeastern Costa Rica as seen intermittently over several years.

Dates	Season	Time of day	<i>Morpho peleides</i>			<i>Morpho granadensis</i>			<i>Morpho amathonte</i>		
			♀ ♀	♂ ♂	T	♀ ♀	♂ ♂	T	♀ ♀	♂ ♂	T
VIII-14-77	rainy	1300	0	0	0	0	1	1	0	1	1
VIII-15-77	rainy	1300	0	3	3	0	0	0	0	0	0
XI-30-78	rainy	1200	0	1	1	0	0	0	0	0	0
XII-1-78	rainy	1130	1	0	1	1 <sup>a</sup>	0	1	0	2	2
XII-2-78	rainy	1100	0	0	0	0	0	0	0	2	2
XII-3-78	rainy	1330	0	1	1	0	0	0	0	6	6
XII-4-78	rainy	1400	1	0	1	0	0	0	0	2	2
XII-5-78	rainy	1000	0	0	0	0	0	0	0	1	1
III-11-79	dry	1000	1	0	1	0	0	0	0	0	0
III-12-79	dry	1000	1	0	1	0	0	0	0	0	0
IX-28-79	rainy	1400	0	0	0	2 <sup>b</sup>	0	2	0	1 <sup>c</sup>	1
X-3-79	rainy	1400	0	1	1	0	1	1	0	1	1
II-12-80	dry	1200	1	2	3	0	0	0	0	3	3
II-13-80	dry	1230	1	1	2	0	0	0	0	1	1
II-20-80	dry	1330	0	0	0	0	0	0	0	1	1
II-21-80	dry	1230	0	0	0	0	0	0	0	1	1
II-22-80	dry	1200	0	2	2	0	0	0	0	1	1
II-23-80	dry	1200	0	1	1	0	0	0	0	0	0
VI-13-80	rainy	1400	0	2	2	0	5	5	0	0	0
VI-14-80	rainy	1400	0	0	0	0	2	2	0	1	1
VI-15-80	rainy	1400	0	0	0	0	1	1	0	0	0
VI-16-80	rainy	1400	0	0	0	0	1	1	0	2	2
II-3-81	dry	1500	1 <sup>d</sup>	2	3	0	0	0	0	0	0
II-4-81	dry	1500	0	1	1	0	1	1	0	1	1
II-5-81	dry	1500	0	0	0	0	2	2	0	1	1
VII-24-81	rainy	1300	1	0	1	0	2	2	0	1	1
VII-26-81	rainy	1300	1 <sup>e</sup>	0	1	0	1	1	0	0	0
Total butterfly sightings:			9	17	26	3	17	20	0	29	29
% rainy season sightings:			46.1%			75.0%			69.0%		

<sup>a</sup> In captivity this female produced 53 viable eggs in two weeks.

<sup>b</sup> In captivity one female produced 8 viable eggs in 8 days, the other 24 eggs in 2.

<sup>c</sup> This male fed continuously for at least one hour.

<sup>d</sup> In captivity this female produced 16 viable eggs in 3 days.

<sup>e</sup> In captivity this female produced 26 viable eggs in 5 days.

as the total number of eggs produced by the average female during her lifetime) than does *M. granadensis*, and that this phenotypic trait is associated with the ability of the former species to colonize a broad range of ecological conditions throughout much of the American tropics. Thus the lower abundance of adult *M. granadensis* at baits reflects a smaller breeding population, rather than a necessarily large population dispersed over large areas. It is interesting to note the similarities in adult abundance between

*M. peleides* and *M. amathonte* in this region. Both of these species are widespread forms throughout the lowland and premontane tropical rain forest region of the Caribbean drainage of Costa Rica, and that ranked abundance with *M. granadensis* is not unexpected (Young 1972a). All three species have single oviposition and legume-feeding caterpillars, conditions that promote widespread distribution. Elsewhere (Young and Muyschondt 1972b) it was proposed that *M. amathonte*, representing the Central American expansion of *M. anaxibia* from South America, with its dazzling blue wing colors in the males, is the dominant form of the genus in lowland tropical rain forests, whereas forms such as *M. peleides*, with more subdued wings, are the dominant representation of the genus at higher forested elevations. *Morpho granadensis* seems to "fit in" by being distributed at an intermediate elevation, and perhaps between the two major faunistic regions for the other forms mentioned above. Given some preliminary information available on these and other species of the genus in Central America, I propose the summary of ecological distributions given in Figure 8. This scheme is meant to be a starting point for further study, rather than a conclusion based on a solid background of field data.

Owing to its relatively narrow geographical distribution in Costa Rica and presumably elsewhere, *M. granadensis* is probably a more ecologically-specialized species of mixed primary-secondary tropical rain forest than the more cosmopolitan *M. peleides*. The inability of the caterpillars of *M. granadensis* to exploit one of the most abundant larval food plants of *M. peleides*, *Mucuna urens*, and their inability to develop successfully on a cultivar such as peanuts, tentatively suggests ecological specialization in a direction away from *M. peleides*. What is lacking is critical data on the scope of larval food plants of *M. granadensis* in zones of overlap with *M. peleides*. If it is assumed that *Machaerium seemannii* is the dominant larval food plant of *M. granadensis*, much of the distribution of this butterfly may be explained by the distribution of this woody vine. Although this vine is abundant at higher elevations in the same region of Costa Rica, where it is exploited by *M. peleides* (Young and Muyschondt 1973), the marked absence of *M. granadensis* from this region suggests the operation of other factors generating this distribution. With an absence of critical biogeographical data, perhaps larval food plant distribution coupled with other factors such as climate play a joint role in limiting *M. granadensis*. Whether or not ecological differentiation within larval food plant populations, in which the defensive chemistry against herbivorous insects is altered geographically, plays a role in the absence of *M. granadensis* from both montane and coastal tropical rain forest zones cannot be ruled out at this time. As pointed out by Ehrlich and Raven (1969), there is a need to consider the evolutionary history of a species in determining patterns of ecological differentiation.

The data on adults suggest that the short, often erratic dry season char-



The species of Morpho butterflies found in premontane-to-lowland tropical wet forest region of northeastern Costa Rica, and their general habits.

SPECIES	MAJOR ADULT HABITAT(S)	FLIGHT HEIGHT RANGE	RELATIVE ABUNDANCE	LARVAL FOOD-PLANT TAXA
<u>M. peleides</u>	various secondary; large forest light gaps	1-3 M	high	several Leguminosae
<u>M. granadensis</u>	advanced secondary; large forest light gaps	1-3 M	low	prob. few Leguminosae
<u>M. amathonte</u>	primary forest	1-6 M	intermediate	prob. few Leguminosae
<u>M. theseus</u>	primary forest	6-30 M	low	prob. few Menispermaceae
<u>M. cypris</u>	primary forest	10-30 M	low	prob. few Leguminosae

Defined here as 0-200meters above sea level.

Fig. 8. A schematic summary of the major ecological attributes for the species of *Morpho* butterflies found in northeastern Costa Rica. Data on habitats, flight ranges, and relative abundance from direct field observations over several years, and larval food plant data from both field and laboratory study, and the literature.

acteristic of this region of Costa Rica does not appreciably affect the population structure of the butterflies. In all three species, adults are active at various times of the year. It is likely that the larval food plants are not deciduous and therefore remain evergreen during dry periods. Thus breeding can be continuous throughout the year. What may vary is the distribution of natural adult foods. I have noticed that during dry periods adults arrive at baits faster than in the rainy season. Increased dryness may result in increased feeding to maintain water balance and it may also result in a decrease in density of suitable foods, which include sweet-smelling rotten fruits and soupy fungal growths (Young 1979, 1980a). Throughout the year, females are rare at baits, possibly the result of a sexual difference in pref-

Table 2. Summary of the major ecological characteristics of *Morpho peleides* and *M. granadensis* in terms of explaining their distribution.<sup>a</sup>

Phenotypic and other characters responding to selection	Determined and/or predicted <sup>b</sup> character states	
	<i>Morpho peleides</i>	<i>Morpho granadensis</i>
(1) Geographical range	widespread	restricted
(2) Local endemism and restriction of gene flow	low*	high*
(3) Distribution across marked elevational gradients	high	low
(4) Ability to occupy highly seasonal regions	good	poor
(5) General spatial patchiness of resident populations over approx. 1,000-meter sections of a region	low	high
(6) Dispersal ability of adults	high	moderate-to-low*
(7) Intrapopulation variation	high*	low*
(8) Interpopulation variation	low*	moderate-to-high*
(9) Habitat selection	generalized (low)	grading into specialized (high)
(10) Main habitat	grades of secondary forest	advanced secondary forest
(11) Colonizing ability	high	moderate-to-low*
(12) Local population density	high	low
(13) Regional breadth of larval foodplants	high	low*
(14) Acceptability of each other's larval foodplants	high	low
(15) Relative abundance of larval foodplants per unit area of suitable habitat	high	low*
(16) Oviposition strategy	single and scattered	single and scattered
(17) Oviposition proneness in captivity	high	low
(18) Predation/parasitism on immature stages	high	high <sup>b</sup>
(19) Overall fecundity (average per female)	high	moderate
(20) Egg-adult developmental time		very similar*
(21) Larval dawn-dusk feeding	present	present
(22) "Bait-ability" of adults	excellent	fair-to-good
(23) Daily turnover of adults at baits	high	moderate
(24) Sex ratio of adults at baits	skewed males	skewed males
(25) Diurnal rhythmicity of adult feeding	present	present
(26) Percent character states in common: 28.0%		

<sup>a</sup> Analyses of these characters should include an examination of breeding populations in both regions of species overlap and non-overlap.

<sup>b</sup> Character states marked with an asterisk are predictions, while unmarked ones are empirical observations from previous studies (Young 1971a, b, 1972a, b, 1973, 1974, 1975a, 1978b, 1979, 1980a; Young and Muyschondt 1973; Young and Thomason 1974) and unpublished data (Young).

erence for feeding on rotten bananas. Rearing studies (Young and Mui-shondt 1973) indicate that sex ratio is near unity in egg batches. The complete absence of female *M. amathonte* from baits may indicate, together with the scarcity of females in the other two species, that females have different feeding habits from those of males. Because observations were made at various times of the day, it is unlikely that females were missed at the baits. Rather, their food requirements may be considerably different from males in all three species, and possibly linked to nutritional demands associated with egg production.

Table 2 summarizes a proposed model for the overall evolution and ecological differentiation of *M. granadensis* and *M. peleides*. This framework is suggested as a means for developing some testable hypotheses on the ecological properties of these two species, a topic of considerable interest since both are members of the same "superspecies" complex and exhibit considerable sympatry at the same time. The proposed model can also be eventually applied to the other species of *Morpho* as natural history data are gathered on them. Basically this model makes some testable predictions about the differences in genetic structure and ecological properties between a pair of species, one of which is geographically and ecologically more restricted than the other in the tropics.

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